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# SHORTER ARTICLES AND DISCUSSION

## HUMIDITY—A NEGLECTED FACTOR IN ENVIRONMENTAL WORK

An admittedly rough but probably fair estimate of the relative interest which has been taken in the relation of the various environmental factors to insects, at least, may be made from the fact that Bachmetjew in his admirable compilation[1] of the work along these lines devotes, in round numbers, four hundred pages to temperature, one hudred and fifty to food and chemicals, seventy to light, forty-five to humidity, fifteen to electricity and magnetism and thirty to mechanical and other factors. Why is it that temperature is given about a third more attention than all the other factors put together? Is it true that it is nearly ten times as interesting or important as humidity?

A partial answer to the first question undoubtedly is that temperature is easily controlled as well as measured, whereas humidity, for example, is not easily controlled and the means of measuring humidity in small containers are untrustworthy and expensive. Furthermore, work with temperature gives results. The unfortunate part is that these results have usually been ascribed wholly to temperature.

In the course of some work at the Carnegie Station for Experimental Evolution I found that I could change to a surprising extent the markings on the larvæ of a moth (*Isia isabella*) by varying the temperature at which they fed and moulted. However, such changes were much more definite when the temperature was kept constant and humidity varied. I did not have the necessary apparatus for getting accurate control of either factor, but I feel confident that temperature had little or no direct influence. It was acting through its influence upon humidity.

It would seem unnecessary to urge upon experimenters such a fundamental principle in the logic of cause and effect, but the fact is that with only two or three exceptions none of the more than a hundred papers having to do with the effect of temperature upon insects tell us anything about the effect of temperature

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[1] "Experimentelle Entomologische Studien vom physikalisch-chemischen Standpunkt aus." Zweiter Band. Sophia, 1907.

*per se.* A few state that the atmosphere was "moist" or "dry," but even then how moist or how dry is not usually mentioned unless it is believed to be saturated or absolutely free from moisture. It is clearly incumbent upon the one who makes such a criticism to show, either by his own work or in a review of that of others, that humidity is a factor of such importance that the criticism is worth the making—especially since the point is so self-evident and has been made in the past. The following notes are an attempt to justify the preceding.

The experiments of many workers show that when lepidopterous pupæ are subjected to abnormal temperature part, at least, of the adults which emerge differ from the normal. The observations have usually been made on color changes, and Fisher[2] especially has shown that warm conditions (36° to 41° C.) produce the same or similar effects as do cold conditions (0° to 10° C.), also that hot conditions (42° to 46° C.) produce effects which are similar to those produced by freezing (—20° to 0° C.). Fisher apparently had no means of successfully controlling the humidity but Tower[3] claims to have had this in his "Investigation of Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*" and he obtained similar results, stating them as follows:

> The result produced by either a higher or a lower temperature is the development of a greater amount of pigmentation and a consequent melanic tendency in variations. This stimulus in both directions to increased pigmentation reaches a maximum between 5° and 7° C. deviation from normal. Beyond these, as the temperature further deviates, there is a rapid fall in melanism, first to the normal, and then to a condition below normal, until a marked albinic tendency is found; and this decrease in pigmentation continues until the zero point is reached, beyond which no pigment whatever is produced. The zero point is reached much sooner, however, in high-temperature experiments than in low.

Tower then gives the results of experiments in which all the environmental conditions, except humidity, are "normal." Normal humidity for *Leptinotarsa decemlineata* is taken as ranging from 43 per cent. to saturation with an average of 74 per cent. The humidity in various experiments ranges from 10 per cent. to saturation. The lowest natural humidity of which I have seen a record is 5 per cent. It occurred in Death Valley, California, where the monthly means for May to September inclusive varied from 20 per cent. to 27 per cent. The annual mean at Cairo, Egypt, is 56 per cent. and at Ghardaia (Algerian Sahara) is 50 per cent. at 7 A.M. and 26 per cent. at 1 P.M. The humidity at Buitenzorg, Java, during the height of the rainy season fluctuates between 70 per cent. and 97 per cent. during the day. Naturally, when dew is being deposited the humidity is practically 100 per cent. It will be seen then that even Tower's extreme averages (see below) are not beyond the range of possibility in nature, although they are as great as it is possible to use in experimental work, since at an average of 34 per cent. humidity only 0.4 per cent. of the larvæ reached the adult stage and atmosphere can not be kept supersaturated.

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[2] See *Archiv für Rassen- und Gesellschafts-Biologie,* 1907, IV, pp. 761–793, for Fisher's statement concerning criticisms of his conclusions.

[3] Carnegie Institution of Washington, Publication No. 48, 1906.

The beetles were seriated according to an arbitrary scale in which "20 equals total melanism and 0 total albinism." It is difficult to suggest a better method of measuring the extent of melanism than this, although we could wish for diagrams to aid us in grasping just what the scale means. I have tabulated the experiments and interpolated the normal data.

| Relative Humidity | | Per Cent. of Mortality | Melanism | |
|---|---|---|---|---|
| Average | Range | | Mode | Range |
| 100 | 100–100 | 90 | 4 | 2–9 |
| 95 | 82–100 | 30 | 7 | 3–11 |
| 84 | 55–100 | 15 | 12 | 7–16 |
| *74* | *43–100* | *?* | *9* | *5–13* |
| 66 | 33–100 | 35 | 11 | 6–18 |
| 60 | 30–100 | 80 | 5 | 3–11 |
| 50 | 25–83 | 92 | 3 | 1–7 |
| 34 | 10–55 | 99.6 | 2 | 1–4 |

It will be seen that mortality increases rapidly as the humidity departs from normal but this can not account for the change in color since the range of melanism is doubled and in three of the experiments even the mode falls below the normal range. As stated by the author:

> The results of experiments with deviations of humidity are almost exactly the same as those which were obtained from experiments with deviations of temperature. Such deviations from the normal either toward an increase or a decrease, produce up to a maximum increased pigmentation and a consequent melanic tendency, but beyond this the effect is reversed, pigmentation is retarded, and the tendency toward albinism becomes more and more pronounced as the deviation from the normal becomes greater.

The point which concerns the present discussion is that not only does humidity have a definite regularly acting influence, but that its results are similar to those of temperature and, as with temperature, plus and minus variations of certain intensities bring about similar effects. If, as has usually happened, the humidity is not controlled in experimental work on the effect of temperature, how can it be said that the observed results are the effect of changes in temperature?

Tower made certain experiments in which both temperature and humidity are abnormal, normal average temperature being taken as 22.2° C. Unfortunately, proof reading or something of the sort was faulty when it came to publication. Experiment 26 would be the most valuable for our present purpose, but the table includes records of relative humidity 35 and 39 per cent. above normal, *i. e.*, relative humidities of 109 and 113 per cent., respectively, if, as in the other experiments, 74 per cent. is ''normal'' humidity. These are clearly impossible. The text figure illustrating this experiment does not help us since humidities are not given and furthermore the temperatures in the figure are rather consistently one degree different from those given in the table. Since there are two errors in text-figure 15, which illustrates the experiments with humidity as the only variable, it is likely that the figure is the thing that is at fault here. Several other similar discrepancies could be pointed out (as, for example, the temperatures in experiment 24, which concerns the combination effect of humidity and temperature) but it is probable that the author's notebook records are correct and the temperature discrepancies in the published report are so slight that we may accept his conclusion. It is

> that when temperature and moisture are the variables in a given environmental complex, the trend of general color modification is controlled by moisture (relative humidity), excepting in conditions where the temperature deviation is so excessive that the ordinary physiological and developmental processes are greatly inhibited. In experiments approximating natural environmental complexes, however, moisture is the dominant factor in influencing coloration.

Even if there were no other reasons for urging the necessity of taking humidity into account, I feel that Tower's work would be ample justification. Before taking up those reasons let us notice several cases where, on account of the striking results of the experiments, we must regret our lack of information as to the real cause or the relation of the several causes.

This same work of Tower is one of them. The effects just noted were merely ontogenetic. However, he made other experiments in which the effect seemed to be passed on by heredity. The factors in the various experiments with *L. decemlineata* were 35°, 45 per cent. and low atmosphere pressure (p. 287); "hot, dry" (p. 288); "hot, dry and low pressure" (p. 288); and "hot, moist" (p. 291), probably 31.2°, 94 per cent. Those with *L. mulitæniata* were 30° and saturation (p. 292 and p. 293); and the one with *L. undecemlineata* was "10 C. above the average and a relative humidity of 40 per cent." The work is of such importance because of its pioneer character that it would be ungracious to complain too strongly, but the fact is that it is impossible to tell from the data given whether the effects are caused by humidity or by temperature or by a combination of the two. Bateson's idea that there are no effects to be explained need not concern us here.

There is a long series of interesting papers starting in 1895 by Fischer. As has already been mentioned, he finds that certain high temperature grades produce effects which are similar to those produced by certain low temperature grades. The conditions of humidity are rarely mentioned, not to say considered. However, he occasionally confesses that they are important, as when he tells us[4] that it is necessary to have the warm air dry and the cold air moist in order to get similar forms of *Vanessa* by the application of moderate cold and moderate heat. I suspect humidity largely enters into the other experiments also for in one with high temperature,[5] which gave the same results as certain low temperatures and presumably high humidity he says the humidity was high.

Like Tower's experiments with beetles these concern color alone. Pictet[6] and Federley,[7] especially, have considered the effect of environmental factors upon the form of lepidopterous scales. Federley calls his work "Temperatur-experimente" and Pictet "Influence de l'Humidité" but neither enables us to differentiate the effects of the two factors, although both obtained striking results. Kominsky[8] modified to a considerable extent not only the color and form of scales but also the form of antennæ, legs and other body parts of Lepidoptera. He exposed the pupæ to 42.5° C., humidity not given; 38° to 39° C. and 42° to 43° C., relative humidity 80; 8° C., "high humidity"; 0° C., "very high humidity"; —7.5 to 5° C., relative humidity 80–90 and 50; and —11° C., humidity not given. For the most part the humidity was high and probably had much to do with the results, but we can not be certain.

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[4] *Algemeine Zeitschrift für Entomologie,* VIII, p. 274, 1903.

[5] *Illustrierte Zeitschrift für Entomologie,* IV, p. 134, 1899.

[6] *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève,* XXXV, Fasc. 1, 1905.

[7] *Festschrift für Palmen,* No. 16, Helsingfors, 1905.

[8] *Zool. Jahrbücher. Abt. für Allg. Zool. und Physiologie,* pp. 321–338, 1911.

All the experiments just considered were made upon pupæ. It should be remembered that only about one fourth of the weight of lepidopterous pupæ consists of solids, and that the only way they can replace fluids lost by evaporation is by chemical changes in these solids. It is probable that they do so to some extent, although this has not been accurately determined. It is known that under normal conditions pupæ lose in weight and the percentage of solids increases. Naturally, a change in the humidity of the surrounding air would modify this physiological process and it is difficult to believe that it has not quite as much effect as changes in temperature, the humidity remaining the same. It is easy to see that, if the air is made more absorptive or less absorptive either by the temperature changes themselves or by other means, and then the physiological activities are slowed or quickened by temperature changes, the effects will be much greater and might easily pass as due entirely to the temperature changes.

The species which have wet and dry season forms in regions where the temperature is fairly constant throughout the year, as well as the tendency for the animals of moist regions to be melanic and of arid regions to be light colored, speak for the important influence of humidity. But there is another point in distribution to be considered. The study of distribution was long, and still is, largely an effort to get the ranges of animals and plants to fit isotherms. When yearly averages do not work, winter minima or summer maxima or accumulated temperatures are tried. The success which often attends these efforts shows that man is very ingenious and also that temperature is really one of the controlling factors, but it does not show that it is the only factor or, in fact, that it has any direct influence.

The areas of grassland and forest in North America cut across isotherms as though they were merely political boundaries but Transeau[9] has shown that if we plot the ratio of temperature to humidity we get a very close correspondence between distribution and climatic factors. Schimper[10] has brought together a great deal of evidence which indicates that, as far as plants are concerned, even the major divisions of the world's surface into arctic, temperate and tropical are fundamentally a question of the demand for and supply of water.

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[9] Amer. Nat., XXXIX, pp. 875–889, 1905.

Furthermore, if recent climatic changes have an effect upon the origin of new characters and the distribution of the organisms possessing certain characters, humidity is deserving of more attention than temperature, since practically the only evidence we have of such changes concerns humidity.

It should not be forgotten that even aquatic organisms are subject to what amounts to changes in humidity. Peat bog plants take on many characteristics of a desert flora, although their roots are covered with water. It is water, however, which is not easily available, because of the chemicals which it carries. It is water which is physiologically dry.

Finally, the great amount of work which has been done upon artificial parthenogenesis and related subjects is, in a way, a study of the influence of environmental factors. The obvious factors concerned have usually been various chemicals but at foundation humidity, in a broad sense, the addition or withdrawal of water by osmosis seems to be a factor of prime importance.

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[10] "Plant Geography upon a Physiological Basis," translated by W. R. Fischer. Oxford, 1903.